

THE PROPER NAME FOR THE GEODUCK: RESURRECTION OF
PANOPEA GENEROSA GOULD, 1850, FROM THE SYNONYMY OF
PANOPEA ABRUPTA (CONRAD, 1849) (BIVALVIA: MYOIDA: HIATELLIDAE)

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INTRODUCTION

In 1849, Conrad described, illustrated, and assigned the name *Mya abrupta* to a new species of fossil bivalve collected from Miocene deposits along the banks of the Columbia River near Astoria, Oregon, during the United States Exploring Expedition of 1838–1842 (Conrad, 1849: 723, pl. 17, fig. 5a, b, USNM 3608; Figs. 1–3). Conrad described it as:

“Subelliptical, slightly ventricose, widely gaping posteriorly. Surface marked with concentric undulations. Beaks separated, nearly medial, slightly prominent. Anterior margin acute, orbiculate; posterior margin abrupt, arcuate, somewhat reflexed; basal (inferior) margin arcuate; dorsal margin short, straight, nearly parallel with the base.”

In 1850, Gould described the valves of a new extant species collected from the Nisqually region of Puget Sound, Washington, during the same expedition and assigned it the name *Panopea generosa* (Gould, 1850: 215, USNM 5894; Figs. 4–7). Gould (1852: 385–386; 1860, pl. 34, fig. 507, 507a) later figured and expanded the description:

“Shell large and ponderous, chalky white, of a somewhat quadrilateral form, the basal and hinge margins being nearly parallel; the posterior extremity broadly truncated a very little obliquely, and the anterior extremity broadly rounded; anteriorly it gapes slightly, but posteriorly it gapes broadly, and the valves are here somewhat everted. The surface is coarsely undulated concentrically, and covered by an obliquely, and somewhat plumosely wrinkled, dirty yellow epidermis. The beaks are sharp and prominent, placed near the middle of the superior margin; the anterior umbonal slope is tumid, the posterior a little compressed. The hinge is rather slender, having a single elevated, erect, obliquely triangular tooth in each

valve, with a pit behind that in the right valve, and a crest-like elevation for the attachment of the ligament behind them. Ligament external and double. Cavity of the beaks profound, muscular and pallial cicatrices broad and well impressed; posterior muscular scar but little broader than the pallial impressions; siphonal sinus shallow, small.”

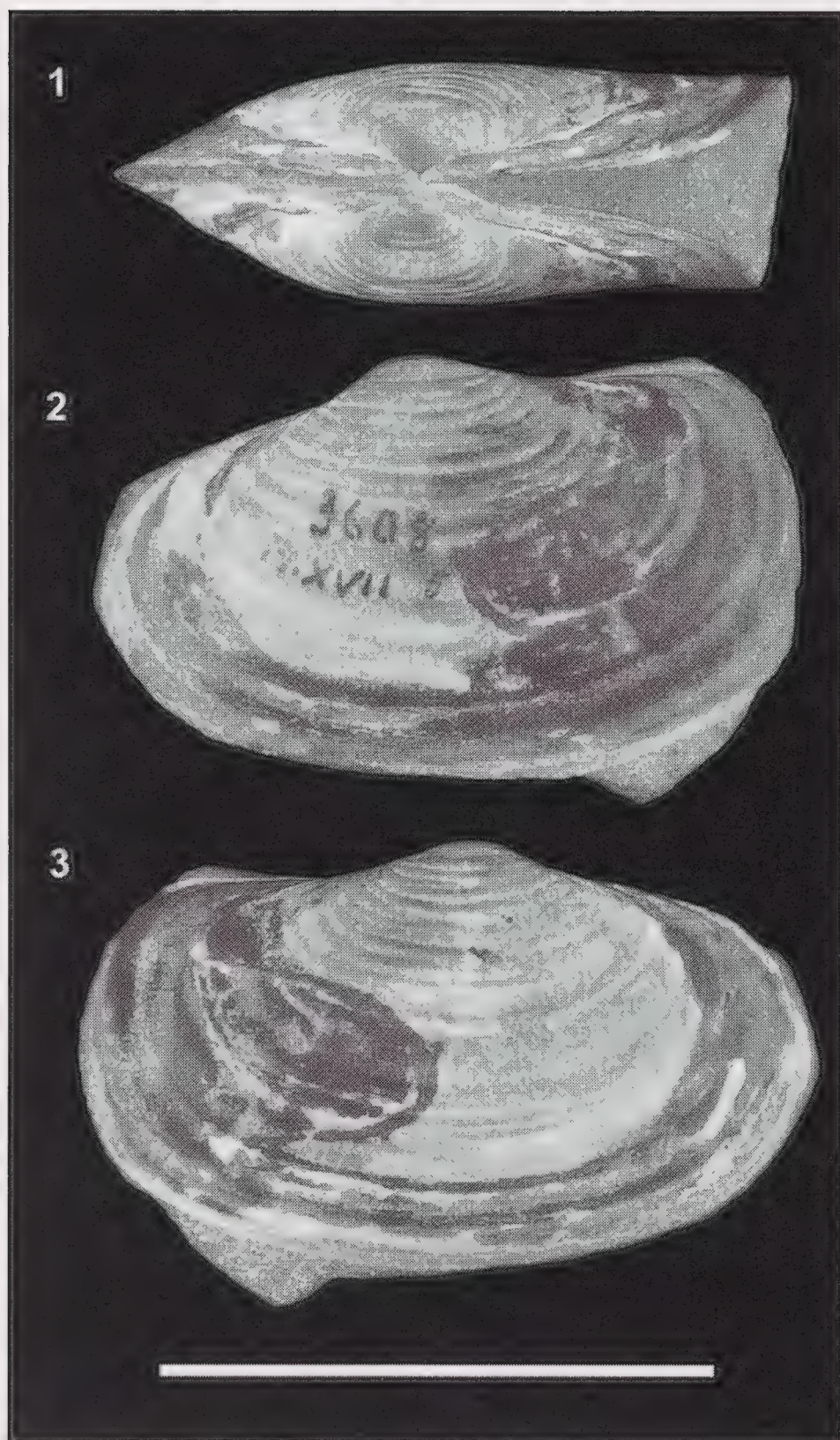
MATERIAL EXAMINED

Holotype of *Mya abrupta*, USNM 3608; holotype of *Panopea generosa*, USNM 5894; *Panopea* spp. (n = 30) in collections of the Burke Museum of Natural History and Culture, University of Washington, Seattle, collected from lower Oligocene to Miocene deposits in Oregon, Washington, and British Columbia, Canada (catalog numbers, some of which include multiple specimens: 04471, 04510, 06650, 06697, 06705, 13348, 13891, 18423, 18892, 18924, 21391, 22341, 24860, 26317, 27512, 27611, 27762, 29556, 42797, 53669, 61705, 73465, 91557, 96501, W485); and more than 4,000 specimens of *Panopea generosa* collected from Puget Sound, Washington, as part of a long-term study of population genetics, maturation dynamics, and disease status.

RESULTS AND DISCUSSION

An important difference between the descriptions of *Mya abrupta* and *Panopea generosa* (see Introduction) is apparent. Contrary to Conrad (1849), Gould (1850, 1852) described his specimen as having an anterior gape, a difference evident in the respective holotypes (compare Figs. 1, 4). While compression during fossilization can lead to an apparent narrowing between the gape the valves along the

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FIGS. 1–3. *Panopea abrupta* (Conrad, 1849), holotype, USNM 3608 (scale bar = 5 cm). FIG. 1: Dorsal view showing the relatively narrow width of the gape of the valve along the anterodorsal margin; FIG. 2: Left lateral view; FIG. 3: Right lateral view. All images © Michael K. Brett-Surman, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution.

anterodorsal margin, compression would in turn accentuate the opposing posterior gape, which is not evident in Conrad's holotype.

The two species were synonymized without explanation by Gabb (1869: 89–90), who used the later name *generosa*. Dall (1898: 830–831) subsequently examined both holotypes, concluding that the two represent different species: *P. abrupta* “seems entirely distinct from the *P. generosa*, being a smaller, more slender, and more equilateral species.” Following concurrence by Arnold (1903: 182–183), Dall (1909: 133) reiterated the differences: “Conrad's type. A smaller, more equilateral, and more slender species than Gould's recent shell.”

Clark (1918: 161–162) described the differences between the Recent and fossil taxa in more detail, using the name *Panopea estrellana* (Conrad, 1857) for *P. abrupta* (Clark was not wholly convinced that the two fossil taxa, *P. abrupta* and *P. estrellana*, were the same):

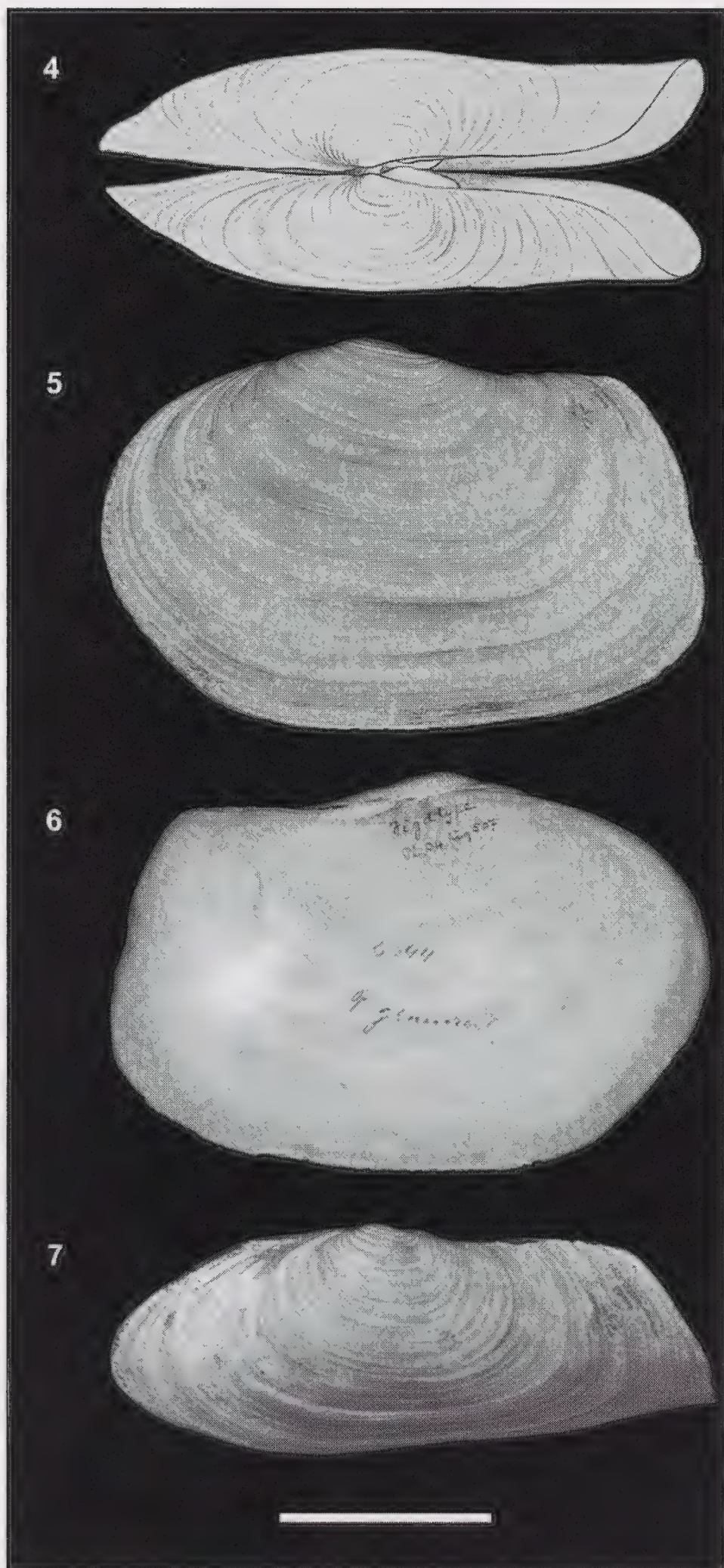
“The Recent species, *P. generosa* Gould, is rather variable in outline and sculpturing; this is also true of the form found in the Lower Miocene and Oligocene, referred to here as *P. estrellana*. Some authors have concluded that the variations of the Recent and Oligocene–Lower Miocene forms are so great that they can not be separated as distinct species. After examining a considerable number of specimens from the Lower Miocene and the Oligocene and of the Recent, the writer believes that the Oligocene–Lower Miocene form is distinct [...]. The most important differences between *P. cf. estrellana* and *P. generosa* appear to be that the former is somewhat longer in proportion to the height and has less conspicuous beaks. The posterior dorsal edge on *P. cf. estrellana* is straight, while on *P. generosa* it is usually concave; on *P. cf. estrellana* there is a wide shallow sinus, which extends from the beaks to the lower side of the truncate posterior end; this is usually absent on *P. generosa*, though appearing on some specimens.”

Clark (1918: 161) indicated further that *P. generosa* is the Recent species: “The writer exposed an imperfect hinge of the right valve of a specimen of *P. cf. estrellana* from the *Agasoma gravidum* beds, apparently enough to show that there are specific differences between it and *P. generosa*.”

Grant & Gale (1931: 424–425) synonymized *P. estrellana* (= *P. abrupta*) and *P. generosa*, stating that “Conrad's figure is not unlike some specimens that would unquestionably be identified as *generosa*.” (These authors used the name *generosa* because they mistakenly thought that the earlier named *abrupta* was a junior homonym of *Pholadomya abrupta* Conrad, 1832 and could not be used. However, the latter is a true *Pholadomya*.) Although Grant & Gale addressed the plasticity of length versus width, the anterior gape characteristics of the two holotypes were not mentioned. Weaver (1943: 262) concurred with this synonymy, but continued to use the name *P. generosa* presumably because of the alleged homonymy.

Moore (1964: 83–84) placed *P. abrupta* and *P. generosa* in synonymy, based in part on a misinterpretation of Dall (1898):

“Dall (1890–1903, p. 830–831, 1898) placed *Mya* [= *Panopea*] *abrupta* in synonymy with



FIGS. 4–7. *Panopea generosa* Gould, 1850, holotype, USNM 5894 (scale bar = 5 cm). FIG. 4: Dorsal view showing the relatively broad width of the gape of the valve along the anterodorsal margin (after Gould, 1860: pl. 34, fig. 507b); FIG. 5: Left lateral view; FIG. 6: Internal view. © Ellen Strong, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution); FIG. 7: Left dorsal view. © Jordan T. Watson, University of Washington.

Panopea generosa Gould because he thought that Deshayes was describing a new species, *Panopoea abrupta*, when actually Deshayes was simply changing the generic assignment of *Pholodaomya* [sic] *abrupta* to *Panopea*. Thus

the proper name for the *Panopea* originally described by Conrad (1849, p. 723) from the Astoria formation is *Panopea abrupta* (Conrad) and the name *P. generosa* should be placed in synonymy."

Finally, Yonge (1971: 26) discussed the biology of *Panopea* in detail, providing a review of the genus, referring throughout his paper to the Recent eastern Pacific species as *P. generosa*, and stating that "the valves are truncated ... and gape widely at both ends."

Our detailed comparison of both holotypes with extant material revealed a striking difference in morphology. The anterior gape, distinctly present in Gould's holotype (Fig. 4) and explicit in his description, but clearly absent in Conrad's fossil (Fig. 1), is also present in every contemporary specimen examined, from small juveniles to the largest adults ($n > 4,000$). While no significant differences in morphology were observed between Gould's holotype and all comparative material examined, Conrad's holotype differs significantly in the ratio of valve width to valve length (Fig. 8).

As mentioned above, a possible explanation for the dissimilarity in gape width is anterior compression during fossilization, which could presumably occlude the anterior gape in the holotype of *P. abrupta*. To investigate this idea, the valves of preserved Recent specimens of a wide range of size and age were compressed anteriorly, producing three clear results: first, the medial valve sections were no longer parallel; second, the region of maximal width occurred at the posterior margin instead of below the umbo; and third, the compressed specimens were no longer orthogyrate. These conditions are not evident in the holotype of *P. abrupta*: the valves are distinctly parallel, the maximal width is medial, and it is orthogyrate, with no prosodetic gape.

The ecologically important Recent species has been commercially harvested since 1969 (Goodwin & Pease, 1991) and farmed since 1996 in the northeastern Pacific (Straus et al., 2008), where it is reported to occur from Cedros Island, Baja California, Mexico (Ignacio Leyva Valencia, Centro de Investigaciones Biológicas dle Noroeste, Mexico, pers. comm., Sept. 4, 2009), to Kodiak Island, Alaska (Coan et al., 2000). A putative junior synonym, *Panopea japonica* A. Adams, 1850, occurs in the northwestern Pacific from Sakhalin Island, Russia to Kyushu, Japan (Coan et al., 2000). The Miocene fossil, *P. abrupta*, has been reported to occur in the coastal ranges of California, Oregon, and Washington (Weaver, 1943).

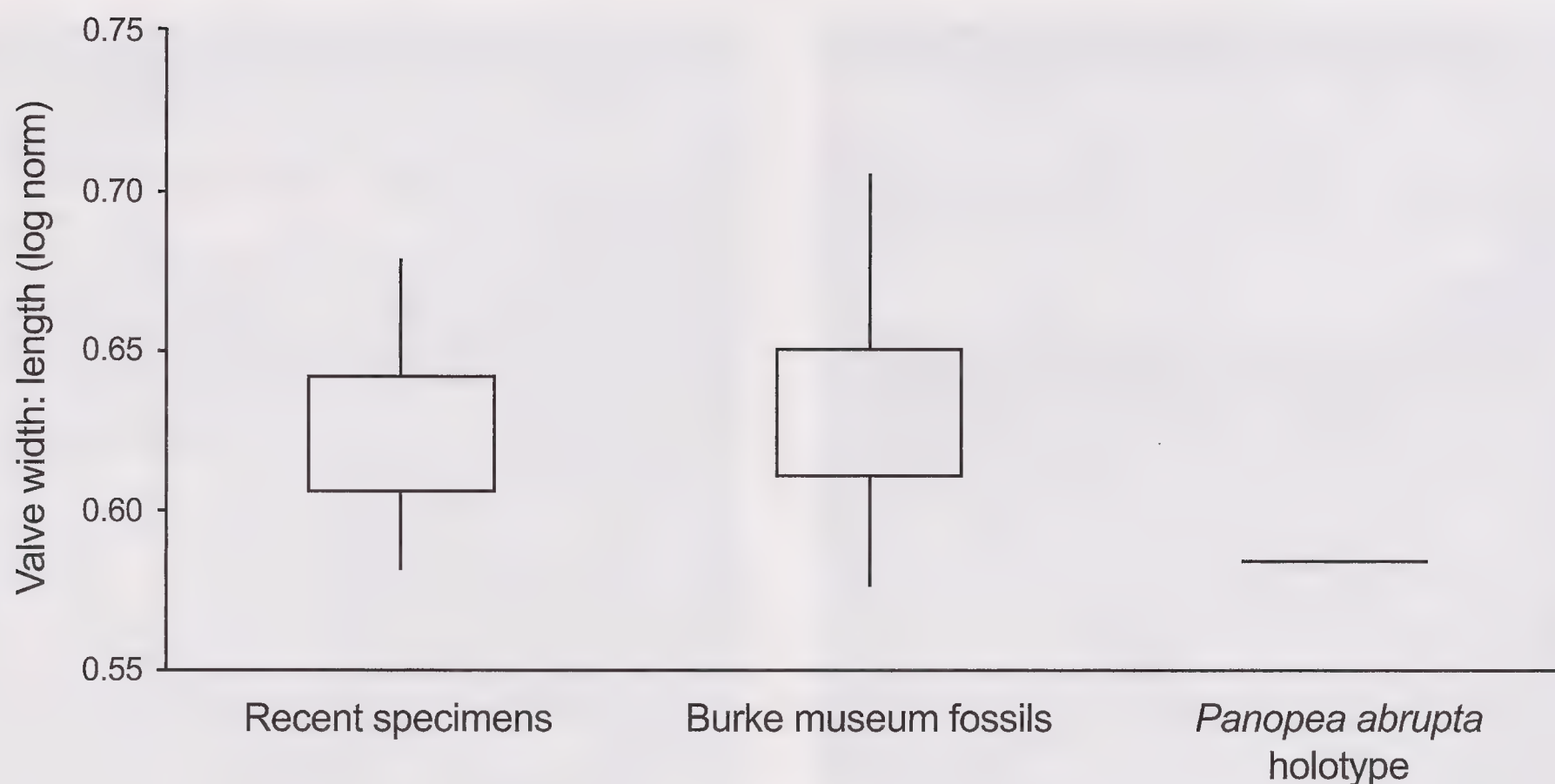


FIG. 8. Box-whisker plot of log-normalized ratios of valve width to valve length for recently collected specimens of *Panopea generosa* ($n = 41$), Oligocene and Miocene material of *Panopea* ($n = 30$), and the holotype of *Panopea abrupta* (USNM 3608).

Of 16 peer-reviewed publications mentioning the Recent species, resulting from a search of the malacological literature from 1969–1982, none used the name *P. abrupta*. But following Bernard's (1983: 59, 70, note 104) synonymization of the two species, based on Moore's (1964) erroneous paraphrasing of Dall (1898), an abrupt shift is evident. From that time to the present (1983 through May 2009), of 44 peer-reviewed publications, only three used the name *P. generosa* for the extant species (Breen & Shields, 1983; Boyer & Goddard, 1999; Boyer, 2001).

The earliest appearance in the peer-reviewed literature of the name *P. abrupta* in place of *P. generosa* was published by Sloan & Robinson (1983); Sloan & Robinson (1984) subsequently mention the synonymy citing Bernard (1983) as the authority. This error has been perpetuated in the scientific literature since 1984, but the differences are clear: *P. generosa*, unquestionably the proper name for the Pacific geoduck, is hereby formally resurrected from the synonymy of *P. abrupta*.

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